HEDONIC RESPONSIVENESS OF COYOTES TO 15 AQUEOUS TASTE SOLUTIONS

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Abstract: Although canid food habits have been well-studied, little is known about taste preferences, per se. We presented sweet, starchy, salty, sour, bitter, and protein tastes to coyotes (*Canis latrans*) in 1-choice 6-hour drinking tests. To evaluate whether preferences might be affected by season, animals were tested in three groups during January, March, and May 1996. Fructose and sucrose were highly preferred, and in most cases, consumption was doubled or tripled, relative to that of tapwater. Quinine hydrochloride was strongly rejected. No other tastes elicited reliable differential responding. These results are consistent with prior demonstrations that dogs prefer disaccharide sugars and the observation that coyote increase liking and chewing of items treated with sucrose. They may also partially explain the preferences that coyotes show for ripe fruit, and their ability to detect subtle differences between ripe and ripening fruit. We infer that disaccharide sugars may be useful additives to baits, and could create some species selectivity. Obligate carnivores (e.g., red fox, felids) are typically indifferent to sugars, and most avian species are either indifferent to or reject these substances. Quinine may be useful as a repellent in some situations. For example, it might be used to reduce coyote damage to drip irrigation hose by biting.

Key words: attractant. *Canis latrans*, coyotes, repellent, taste.

INTRODUCTION

Although canid food habits have been well-studied (e.g., Fazzina 1978, Hilton 1978, Kuo 1967), little is known about taste preferences, per se (c.f., Dixon 1925). Most of the available data is neurophysiological (e.g., Boudreau et al. 1985, Ferrell 1984a), or focused on a particular quality (e.g., sweet, Ferrell 1984b). Moreover, nearly all experimentation has focused on dogs (*Canis familiaris*; e.g., Beidler et al. 1984). While there is no reason to expect that coyotes (*Canis latrans*) differ substantially from dogs, the existence of a comparative data base would be useful. In addition, knowledge of coyote taste preferences would aid in the development of selective baits for the delivery of vaccines and other medications (Linhart et al. 1968, Linhart et al. in press).

We designed the present experiment to explore the hedonic responses of coyotes to a variety of substances representing six taste quality domains (i.e., sweet, starch, salt, sour, bitter, protein or "umami"). All stimuli were presented in 1-choice 6-hour drinking tests.

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MATERIALS AND METHODS

Subjects

Fifteen adult (≥ 1 year old, 8 males, 7 females) coyotes served as experimental subjects. Animals were randomly selected from coyotes maintained at the Millville Predator Research Facility of the National Wildlife Research Center.

Stimuli

Table 1 lists the 15 taste stimuli and their concentrations (Table 1). Selections included three sugars (sucrose, fructose, maltose), one starch (polycose), three bitters (quinine hydrochloride, denatonium benzoate, sucrose octaacetate), three sours (citric acid, acetic acid, hydrochloric acid) and three salts (sodium chloride, potassium chloride, ammonium chloride). Also included were two protein or "umami" tastes. One of these tastes was comprised from a 5:1 mixture of monosodium glutamate and inosine 5'–monophosphate (Kawamura and Kare 1987). The other was a proprietary attractant formulated from meat protein (Hills' Science Diets, Topeka, KS). All 15 stimuli were presented in aqueous solution.

Procedure

Animals were randomly assigned to three groups ($n=5$/group). The first group was tested in January, 1996; the second, in March, 1996; and the third, in May 1996. Our aim was to determine if seasonal differences in taste preference might exist. In dogs, both feeding and drinking are influenced by season, most likely as a result of changes in ambient temperature (Rashotte et al. 1984).

All animals were tested in kennels (dimensions: $3.6 \times 1.2 \times 1.8$ m). Prior to treatments, each coyote was accustomed to drinking from a sipper tube mounted in the center of the front panel of its kennel. At 0800 daily, a graduated cylinder attached to the sipper tube was filled with tapwater. Fluid levels in the cylinder were checked and replenished as needed at 2 h intervals for 6 h. Consumption was recorded to the nearest ml. Overnight,

animals were provided ad libitum access to tapwater. The adaptation period continued for 5 days.

After a 2 day rest period, the treatment period began. Each animal received a different, randomly selected order of the 15 taste solutions, one solution per day for 15 days. As in adaptation, solutions were replenished as necessary at 2 h intervals. At the end of the 6 h period, consumption was recorded.

Analysis

Consumption was evaluated in a two factor analysis of variance with repeated measures over taste solutions. The independent factor was groups. Mean consumption of tapwater during the adaptation period was included in the analysis as a level of the repeated measures factor. Subsequent to the omnibus procedure, Tukey tests (Winer 1962) were used to isolate significant differences among means ($p<0.05$).

RESULTS

There were significant differences among groups ($p<0.001$). Post-hoc tests showed that coyotes tested in January drank less than those tested in March, and those tested in March drank less than those tested in May. There were also significant differences among taste solutions ($p<0.001$). All groups showed significantly greater consumption of sucrose and fructose than any other stimulus (Fig. 1, $ps<0.01$). Conversely, no group drank more quinine hydrochloride than any other taste. In every case, quinine consumption was significantly less than that of tapwater ($p<0.01$). There were no other significant differences ($p>0.25$).

DISCUSSION

Coyotes showed strong preferences for fructose and sucrose, in most cases doubling or tripling intake relative to that of tapwater. We believe that these preferences were mediated by -taste rather than post-ingestional characteristics. First, our casual observations suggested that increases in consumption were immediate. Second, other test substances (e.g., Hill's attractant, maltose) contained as many or more useable calories than fructose or sucrose, yet animals showed no preference for them. Finally, our results are consistent with evidence that (a) dogs show strong preferences for these disaccharide sugars (Grace and Russek 1969, Ferrell 1984b, Stanley et al. 1963); and (b) coyotes increase licking and chewing of items treated with sucrose. One apparent inconsistency along these lines is evidence that dogs show significantly stronger preferences for sucrose or glucose than they do for fructose (Chao 1984). Our data suggest that coyotes' preferences for sucrose and fructose are equivalent. These results may partially explain the preferences that coyotes show for ripe fruit, and their ability to detect subtle differences between ripe and ripening fruit (Kleiman and Brady 1978).

All coyotes showed low consumption of quinine hydrochloride, although consumption of denatonium benzoate and sucrose octaacetate were not different from consumption of tapwater. We infer that only quinine was aversive. This result is consistent with previous demonstrations of marked interspecific variation in responsiveness to substances that humans characterize as
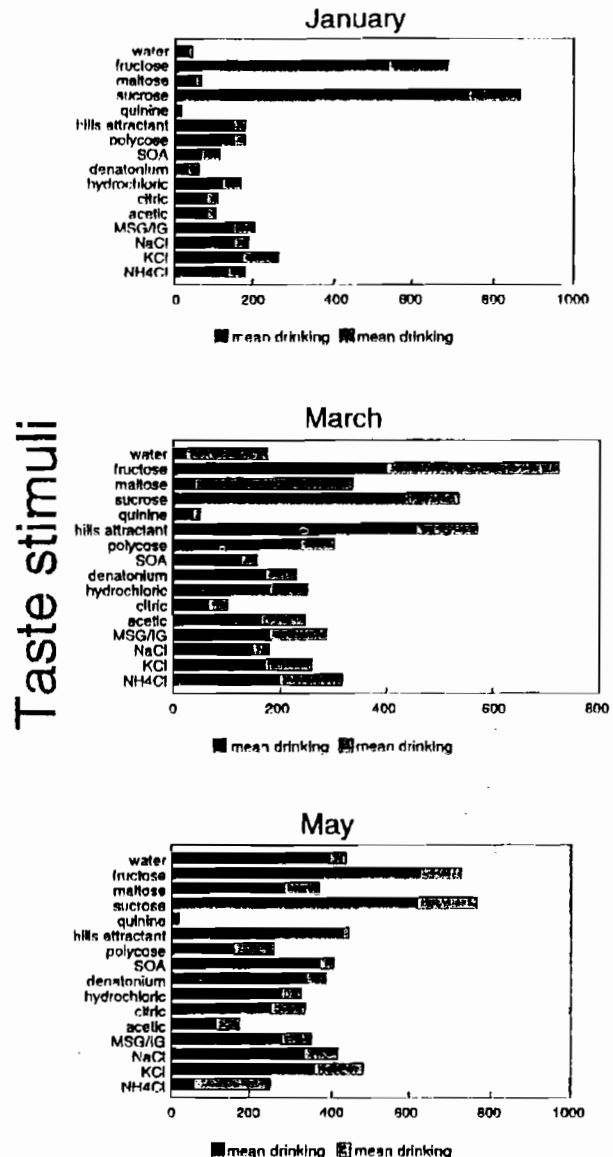

Fig. 1. Mean drinking (± standard errors of the means) by coyotes of 14 taste stimuli in aqueous solution and tapwater in 6 h 1-choice tests.

bitter (Beauchamp and Mason 1991). Although the explanation for this variation remains obscure, it is possible that differences in bitter sensitivity depend upon the feeding ecology of the species in question (Jacobs et al. 1978). In addition, there is good evidence that bitter sensitivity is genetically determined (Lush 1991, Whitney et al. 1991).

None of the salts tested had any effect on response. Although our data do not bear directly on this issue, there is evidence that carnivores are generally insensitive to sodium chloride, perhaps

because their diets are salt-replete (Beauchamp and Mason 1991).

No sour taste reduced consumption. This result was unanticipated, given the strong preference that coyotes displayed for fructose and sucrose. A priori, we had expected that preferences for sweet substances would be linked with the rejection of sour tastes (Beauchamp and Mason 1991). Our reasoning was that if sweetness could serve as a signal for ripe fruit, then sourness might serve as a signal for unripe fruit.

The finding that coyotes showed no strong preference either for protein taste (monosodium glutamate and inosine 5'-monophosphate) or the Hill's attractant was predictable on the basis of the available evidence. Others have shown that monosodium glutamate, proline, and unspecified meat flavor potentiators fail to increase biting and licking by coyotes (Fagre et al. 1981). Although the underlying explanation remains obscure, several possibilities exist. One explanation is akin to that provided above for the lack of response to salt (i.e., coyote diets are normally protein-replete, just as they are salt replete). Alternatively, it may be that the coyote's ability to taste disaccharide sugars precludes an ability to detect protein flavors. Boudreau (1986) has argued that amino acid-sensitive fibers in carnivores are identical to sweet-sensitive fibers in omnivores, the difference being that the former do not respond to simple carbohydrates. It follows that sensitivity to simple carbohydrates may interfere with amino acid sensitivity. Indeed, Boudreau et al. (1985) reported that omnivores (e.g., rats) that detect simple sugars are less sensitive to amino acids than obligate carnivores (e.g., domestic cats).

Finally, there was no evidence of differential responding towards polycose. This lack of response is consistent with the possibility that coyotes do not respond to starch tastes as rodents and some other animals do (Sclafani 1991).

MANAGEMENT IMPLICATIONS

While differences in taste responding may exist between captive and free-ranging coyotes (perhaps as a result of experience), the effects are probably quantitative rather than qualitative (Griffin et al. 1984). Accordingly, our results suggest a variety of testable, practical implications. One is that sugars can be used to enhance bait acceptance (Jacobs and Sharma 1969) by coyotes as well as other omnivorous canids including dogs (Ferrell 1984b) and jackals (Fall 1985). Golden jackals (*Canis aureus*), for example, cause substantial damage to sugar cane (Haque et al. 1984). During the harvest season, damage is significantly reduced when jackals congregate at molasses preparation sites. When sugar processing activities stop for the night, jackals visit sites and consume spilled residues. Molasses may represent an economical and selective bait for this species.

The use of sugar as a bait also may result in some species selectivity. Obligate carnivores (e.g., red fox, felids) are typically indifferent to sugars (Ewers 1973, Jacobs et al. 1978), and most avian species are either indifferent to or reject these substances (Mason and Clark, in press), the possibility exists that sugar-based baits may be relatively species-selective. One caution in this regard is the obvious potential for sugar to

Table 1. Stimuli and their concentrations in aqueous solution[1].

Substance	CAS Number	Concentration (% m/m)
Sucrose	57–50–1	10.00
Fructose	57–48–7	10.00
Maltose	69–79–4	10.00
Polycose[2]	none	0.60
Quinine hydrochloride	130–89–2	0.04
Sucrose octaacetate	126–14–7	0.04
Denatonium benzoate	3734–33–6	0.04
Hydrochloric acid	7647 01–0	0.04
Citric acid	77–92–9	0 04
Acetic acid	64–19–7	0.04
Monosodium glutamate and inosine 5'-monophosphate[3]	142–47–2–58–63–9	10.00 2.00
Sodium chloride	7647–14–5	6.00
Potassium chloride	7447–40–7	3.00
Ammonium chloride	12125–02–9	2.00
Hill's attractant	none	2.00

[1]Stimulus concentrations were selected on the basis of Mason et al. 1991 and Ferrell 1984. [2]Polycose is a corn starch hydrolysate that contains approximately 91% polysaccharides, 7% maltose, and 2% glucose by weight (Sclafani 1991). There is evidence that rodents and perhaps some other mammals have specialized receptors for a distinct starch taste. [3]Monosodium glutamate and inosine 5'-monophosphate, when mixed in a 5:1 ratio, produce "umami", or protein taste (I. Ramirez, Monell Chemical Senses Center, pers. commun.).

increase the palatability of baits to insects. This is a potentially serious problem; in tests conducted in the southeastern and southwestern United States, fire ants (*Solenopsis* sp.) frequently consume large numbers of baits (S.B. Linhart, Southeast Cooperative Disease Study, University of Georgia, pers. commun.).

The present results also have implications for coyote repellents. Quinine hydrochloride may be useful as a nontoxic aversive agent in certain situations. For example, coyotes damage drip irrigation hose by biting. In Fresno County, California, such damage exceeds $200,000 annually (J. Rinder, California Department of Agriculture, pers. commun.). Although the motivation(s) for this behavior remain unclear, there is evidence that treating hose with mammalian repellents such as capsaicin can reduce damage (Werner et al., unpubl. ms.). Quinine hydrochloride would be easier to apply and handle than capsaicin, and also less expensive.

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